

IOPC conference, 17-19 June 2014, Bali Convention Center, oral communication.

Title :

Occurrence of potassium location in oil palm tissues with reserve sugars: consequences for oil palm K status determination.

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## Abstract

In some fertilizer trials for oil palm, it is observed that potassium leaf content was not in concordance with potassium application. In some cases no « leaf » response is observed (leaflet potassium content from leaf rank 17 according to specific LD IRHO method) whatever the K level. Agronomists have suggested to look for potassium content in others organs like rachis, showing best adjustment between K content, yield and K application; This K content difference between rachis and leaflets may be related to their different metabolic role for the plant; When leaflets are devoted to photosynthetic acquisition of carbon for the whole plant, rachis play obviously a role in photosynthetic product transportation; Potassium is often mentioned as involved in sugars translocation. In order to explain K content variations within organs, an experimental observations design has been elaborated on a factorial fertilizer trial (ALCP10, factorial  $K^4 \times Ca^2$  in North Sumatra) involving precise samplings on vegetative organs as leaflets petioles, rachis, trunk and roots as well as fruits, spikelets and bunch stalk. Both mineral content analyses and sugars content (soluble sugars and starch) were performed on a total of 36 oil palm trees belonging to two different contrasting genetic materials. For strengthening our hypotheses, two other set of data were overviewed for K and sugars locations; The first one is a complete dissection of a crown from very young bud leaf stage until old leaves, the second is an exploration of sugars reserves in the crown in North Sumatra conditions. Maximal K mineral content was observed in trunk bottom (for all planting material and treatment) when soluble sugars are high and starch low. Generally it has been observed that potassium is high in petiole of very young leaves (1 to 3) and increasing in bunch rachis until fruit maturation. Leaflets of young leaves (rank -2) contain more potassium than leaflets at rank 17 due to their high proportion in reserve sugars before starting strong photosynthetic activity. Hypothesis is merging from a high co-occurrence of K with soluble sugars in oil palm (most probably glucose) which are involved in the reserve mobilization to elaborate not only bunches but also new young leaves. An inverse relation is found between K concentration and starch. It seems that equilibrium between starch and soluble sugars content at organs scale and the K level are a key to elaborate a clear K nutrient status for oil palm.

Key words : Oil palm, Potassium, Mineral nutrition, Sugars reserves, Leaf diagnosis, Plant tissues

# INTRODUCTION

Potassium is a key major element in mineral oil palm fertilization. In agronomy, K is known to play a role in fruits development and obviously has a direct effect on oil palm yield in relation with the increase of bunch weight and bunch number. It is currently admitted and observed that potassium requirements for mature palms may vary between 0.3 and 3.0 kg K palm<sup>-1</sup> yr<sup>-1</sup> (Ng and Thong, 1985). K requirements for oil palm is depending on soil properties, local ecological conditions (flooding or water deficit, sunshine, temperature, elevation...), plantation age (Jacquemard et al., 2002) and planting material requirement as demonstrated recently (Jacquemard et al., 2009, Ollivier et al. 2013).

Normally, based on the Leaf Diagnosis, "LD" (which is the mineral content of the leaflets at rank 17 related to yield and fertilizer application), K mineral apply in plantation which is mostly under KCl form, is susceptible to cover total plantation requirements whatever other condition.

Despite a great accuracy of the LD method, in some fertilizer trials, it was observed that potassium leaf content was not in concordance with potassium application (Dubos et al., 2010). In some cases no « leaf » response is observed whatever the K level. Some agronomists have suggested to look for potassium content in others organs like the rachis (Wilkie and Foster 1989; Foster and Prabowo, 2002; Foster, 2003), showing best adjustment between K content, yield and K application;

This K content difference between rachis and leaflets may be related to their different metabolic role for the plant; When leaflets are devoted to photosynthetic acquisition of carbon for the whole plant, rachis play obviously a role in photosynthetic product transportation. Potassium is often mentioned as involved in sugars translocation (Gérardeaux, 2009). At the plant level, K<sup>+</sup>, which is an important "free" action in all tissues, is known to circulate quickly in the cytoplasm as the same time with carbohydrates between source and sink organs. Normally K plays a role in the transformation of the light into chemical energy during CO<sub>2</sub> fixation. It is involved in the activation of enzyme responsible for starch synthesis, and the translocation of photosynthetic product from source (leaves) to sink tissues (mainly inflorescence). Its absorption by the roots is through a concentration gradient.

The present work aims to understand, firstly, K different accumulation pattern between sink and source organs for oil palm. The study will focused especially on leaflets, rachis and trunk. The second aim of this study is to propose an analyse of the K status of oil palm trees in relation with carbon metabolism (photosynthesis product and reserve sugars) in order to improve K allocation knowledge and allow better adjustment of the actual LD.

To explain K content variations within organs, experimental observations (K and sugars analyses) design has been elaborated on a factorial fertilizer trial (ALCP10, factorial K<sup>4</sup>xCa<sup>2</sup> in North Sumatra) involving precise samplings on vegetative organs as leaflets petioles, rachis, trunk and roots as well as fruits, spikelets and stalk. For strengthening our investigations on K and sugars allocation, two other sets of data were also overviewed; The first one is a complete dissection of a crown from very young bud leaf stage until old leaves (Quencez, 1992, unpublished), the second is an exploration of sugars reserves in the crown, along ranks, under North Sumatra conditions (Lamade et al, 2009).

## Material and methods

Three different sources of experimental data are used in this paper.

The first data source, is a part of the ISOPALM2 project<sup>1</sup>, conducted on a fertilizer trial, in a SOCFINDO estate (Aek Loba, rainfall 2300 mm, altitude : 35 m a.s.l, ALCP10 : K<sup>4</sup>CA<sup>2</sup> subdivided with 4 progenies (split-plot) with 6 replicates, planted in 2004, K fertilizer treatments started in 2008.

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<sup>1</sup> ISOPALM2 project : Characterization of mineral fluxes N-K for oil palm under sumatran conditions. CIRAD-Palmelit project.

Details : K0 =0.0 kg ;K1 = 0.5 kg K2 = 1.5 kg ; K3= 4.5 kg KCl/tree/yr. Ca0=DAP-Kieserite; Ca1=TSP/RP-dolomite, well described in Ollivier et al. 2013.Only two contrasting progenies, A and B, (Table 1) will be used to in the present work (total of 2 x 18 oil palm trees belonging to A and B, under K0,K2 and K3). A is supposed to be K+ (K leaflets content is high) when B is supposed to be K- (K leaflets content is low). The local ecological conditions are supposed to be potential for oil palm growth and development according to Corley and Tinker (2007).

A	BB 6518 D x LM 12989 P
B	BB 8314 D x BB 8847 P

Table 1. A,B progenies tested in ALCP10 fertilizer trial.

Observations and measurements: in ALCP10, trees samplings were performed on all plant tissues. Concerning the leaflets and rachis, samples of fresh matter were collected along 10 segments (Fig.1), on the rachis, from “C” to “A” point, at the same time of leaf area determination (see method of Tailliez and Koffi, 1992) all on leaf rank number 17. Then, samples were gathered in 4 sections (1-2,3-4-5,6-7,8-9-10). For the petiole, 5 cm length samples were collected at the middle. A complement sampling was undertaken along the spiral 1. Especially for the rachis samples, a distinction was made between the green epiderm and the white parenchyma. For the trunk : 3 different zones were investigated. The base (bottom), at 50 cm of the top soil, the middle, at half height of the total trunk length, the top (trunk up), at the edge of the leaf rank number 33. Samples in trunk were taken with a Pressler auger. Bunches (fruits, spikelets, bunch stalk) and roots were sampled too. Samples were divided in two parts. One part was conditioned (dried in oven following adapted procedure) and send, for mineral analysis, to CIRAD laboratory (CIRAD,US 49, Montpellier, France). Spikelets, bunch stalk and fruits analyses were performed to BLRS (PT Lonsum Sumatra). The other part, after being immersed in liquid nitrogen

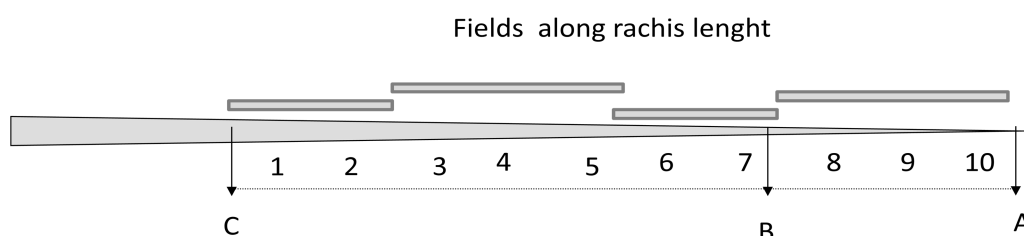


Fig. 1. Rachis diagram divided in 10 equal sections between C and A points.

and softly dried was analyzed , for the starch content (in mg g<sup>-1</sup> of DW) in ESE laboratory (Ecology-Systematic-Evolution, University of Paris XI, Rosary, France) for the soluble sugars (sucrose, glucose, fructose) at the PMM platform (*HPLC* method, IBP, University of Paris XI, Orsay). All analyses used in this work were done on samplings done in 2011.

The second set of data is originated from an important mineral sampling work performed on the material LM2T x D10D in La Mé Oil Palm Research Station (Ivory Coast, 5°25N, 3°50 E, altitude : 75 asl, plot E70, planting 1973, annual rainfall 1486 mm, radiation : 14 MJ m<sup>-2</sup> day<sup>-1</sup>) dealing with complete crown dissection. In this experiment, at least, two complete dissection of adult oil palm crowns were performed (from rank -8 until rank 41, leaves are divided in leaflets, rachis, petioles), as well as trunk, and bunch components. All parts were submitted to standard mineral analyses (N,P,K,Mg Ca, Cl) under I.R.H.O. procedures (Ochs and Olivin, 1977).

The third set is a part of ISOPALM1 project<sup>2</sup> conducted at Aek Pancur Research Station (3°30'N,98°48'E, North Sumatra, altitude : 25m asl, Indonesian Oil Palm Research Institute; Radiation : 16,4 MJ m<sup>-2</sup> day<sup>-1</sup>, rainfall over 2000 mm) on clonal material (MK60) equivalent to LM2T x D10D. Samplings and metabolic analyses were well described in Lamade et al. 2009 .All trees sampled were morphologically characterized with the leaf area, rachis length, trunk height and trunk diameter, in addition with the specific leaf weight (SLW) and trunk density in order to estimate individual biomass.

#### *Statistical analyses*

For the first set of data, mixed analyses of variance tests were performed on K content (for A and B progenies, on different plant tissues, on all leaf ranks, under K0,K2,K3 treatments and all interactions) (mixed procedure, SAS Inc., Cary, NC, USA). For other data sets, both mixed and regular ANOVA were used (ANOVA procedure, SAS). All means comparisons were performed with the Tukey 's test with P<0.05. Means in figures are presented with standard deviation (SD) divided by  $\sqrt{N}$  (N : number of samplings).

## Results

### *K allocation at tree scale*

#### 1. Variation of K content in different rachis tissues

Concerning the data first set, results of ANOVA (Table 2) showed strong effect of both rachis and progenies on K mineral content. The first important observation is that K in rachis, is mainly localized in the white parenchyma where phloem-xylem vessels are situated. On these results, it is possible to see significant difference between A and B progenies with A showed higher K content than B in all rachis tissues.

variables	DF	F value	Pr>F
tissues	2	26,2	***
progenies	1	35,64	***
interaction	2	3,89	0,025+
	A(K+)	B(K-)	
epiderm	0,837±0,27	0,528±0,27	0,677±0,31 c
mix	1,45±0,45	0,84±0,36	1,136±0,50 b
parenchyme	2,15±0,79	1,13±0,36	1,62±0,78 a
	1.44 (a)	0.819 (b)	

Table 2. ANOVA on K content in different rachis parts for A and B progenies: epiderm and parenchyma. "Mix" is a mixing of both tissues kind. a,b,c means comparisons at P<5%.

#### 2. K, N, K/N content along the rachis length from C to A

N and K analyses have been proceeded along rachis from C to A point (a total of 4 different « sections ») with samples as a mix of epiderm and parenchyma. K, contrarily to N content which increase from C to A (Fig.2), is not significantly variable (ANOVA , Table 3) along the rachis length. Both the progenies and the K level treatment has an effect on K content (Table 3, Fig.2).

<sup>2</sup> ISOPALM1 project, Ecophysiological Study in Oil Palm Yield using Carbon Isotope Discrimination , collaborative project between IOPRI, CIRAD and UPS XI.

N content	DF	F	Pr>F
Progeny (A,B)	1	3.82	n.s.
Klevel (KO,K2,K3)	2	11.96	***
Rachis sections	3	52.67	***
K content	DF	F	Pr>F
Progeny (A,B)	1	89.9	***
Klevel (KO,K2,K3)	2	20.64	***
Rachis sections	3	1.24	n.s.

Table 3. ANOVA on effect of" rachis location" (rachis sections) on N and K content. For rachis, samples here are a "mix" of epiderm and parenchym.

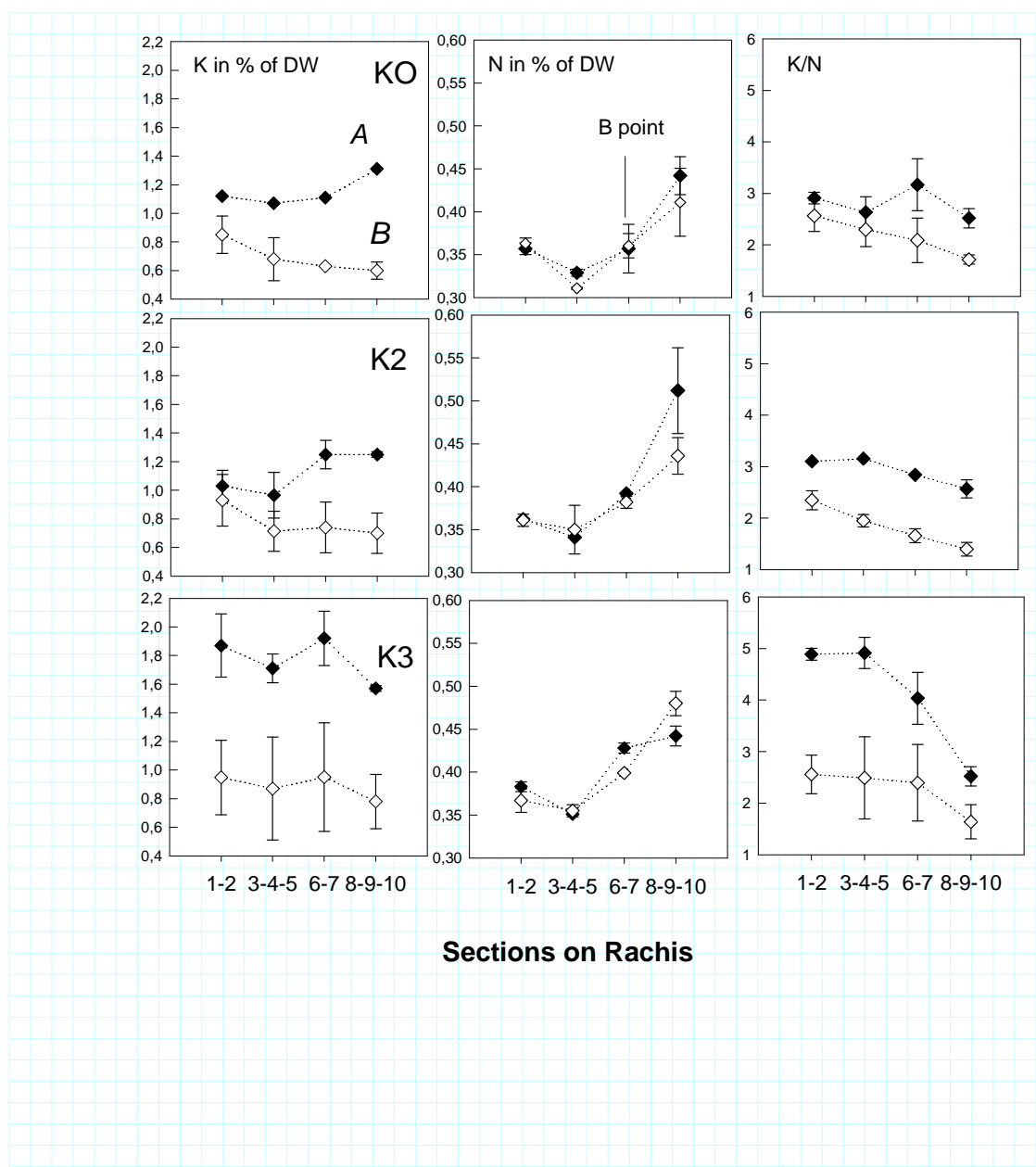


Fig.2. Variation of K and N content in % of DW,as well as K/N along rachis length. For K with A and B progenies under KO,K2 and K3 treatment in ALCP10 trial.

On Fig. 2, it is possible to notice that there an increase of the difference for K content between A and B progenies with the K level. A progeny seems to accumulate more K in rachis than B under K3 application. Low nitrogen content is observed in rachis compared to leaflets (2.3%) whatever the K level. Higher N content observed in last section near A point is maybe due to high N concentration in “green epiderm” which more important proportionally to parenchyma in last section (8-9-10). If no difference are observed for N content along rachis between the two progenies, strong differences whatever the K level are noticed for the ratio K/N.

### 3. Variation of K among heterotrophic and autotrophic organs

Important results on the data first set are concerning the comparison of K content among plant tissues. If all effects studied (K levels, progenies, organs) are highly significant (Table 3), organs is the most important discriminant factor for K mineral content.

<i>Proc mixed</i>				
	<i>numdef</i>	<i>dendef</i>	<i>F value</i>	<i>Pr&gt;F</i>
rep	2	4	4,45	ns
Niv K	2	4	8,6	*
Progenies	5	6	15,69	***
organ	2	162	283,67	***
croist*niv K	2	6	0,12	ns
organ*prog	5	162	7,07	***
organ*niv K	10	162	4,21	***
organ*prog*niv K	10	162	1,75	ns

Table 3. Effect of tissues origin on K content in DW. *Proc mixed* SAS software. With nivk as K treatment K0,K2,K3; progenies as A and B, organs as leaflets, rachis, petioles, trunk up, middle and bottom, roots, spikelets, stalk, fruits.

For the vegetative tree part, potassium allocation shows, whatever K treatment and progenies, a higher concentration in heterotrophic tissues compared to autotrophic one (Fig. 2). Rachis and petioles are enriched in potassium compared to the leaflets. A gradient could be observed from the trunk bottom (high K content around 3%) to the trunk top (2.5%) until the leaflets (0.6 %). Roots are not particularly rich in K with a quite low content (0.6%).

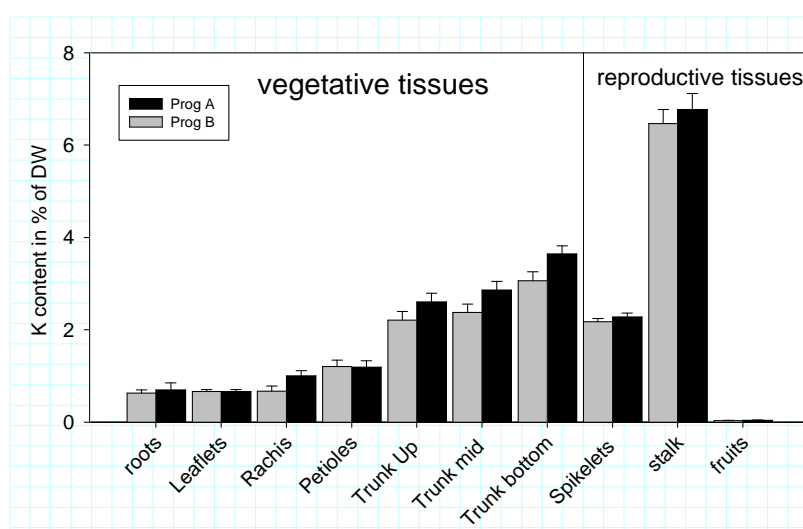


Fig.2. Different K (in % of DW) repartition among vegetative and reproductive organs for oil palm trees in ALCP10 trial for A and B progenies. Autotrophic tissues : leaflets; Heterotrophic tissues : all others. Rachis and petiole contained both.

Concerning the potassium content in mature bunches, a remarkable high K content (7%) is observed in the stalk (the branch of the bunch). The spikelets present also high K content (3%) but less is noticed in fruits (under 0.04%).

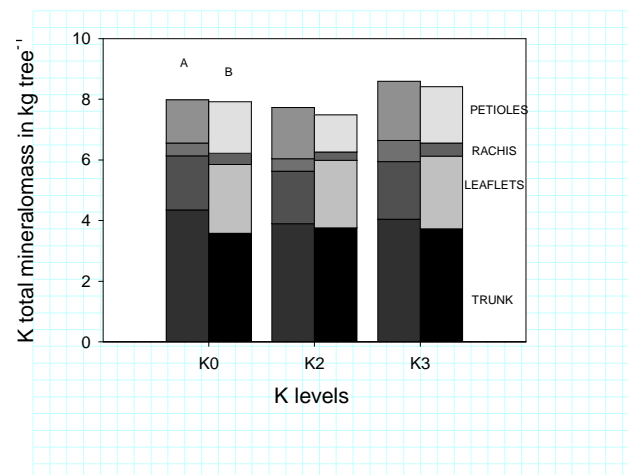


Fig. 3. Total amount of K (in kg tree<sup>-1</sup>) in the upper vegetative tree part for A and B progenies under K0,K2 and K3 treatment. Analyses done on samplings 2011.

The estimation of the total amount of K contained in the biomass -the mineralomass- (Fig.3) is informative of the actual K stock in the oil palm trees studied. It is the reason why, we did estimated for A and B under all K levels, the K mineralomass of the vegetative upper parts of trees studied. The bigger K stock is found in trunks (from 3.5 to 4.3 kg K tree<sup>-1</sup>) and in leaflets biomass (1.7 to 2.3 kg K tree<sup>-1</sup>). The petioles are also an important reserve organ for potassium (from 1.2 to 1.9 kg K tree<sup>-1</sup>).

#### 4. Variation of K content with leaf ranks

Another illustration of K specific allocation among the crown is given by the variation of K content along leaf age (Table 4). Most of the time, if the K content in leaflets is quite low at leaf rank 17 (the rank sampled for LD, here 0.670 %), significant bigger K content is noticed in the young leaves –leaf rank 1 : 1.6% (from rank 1 to 5) which are still heterotrophic compared to adult leaves (form 8 to 33). The leaf rank 9, shows significant higher K content (0.854 %) (Fig.4) than 17 and older leaves (33 : 0.51%) in relation with higher photosynthetic rate in rank 9.

source	DF	F values	Pr>F
progenies	1	0,02	ns
Niv K	2	1,59	ns
rank	5	76,2	<0.0001
prog*niv K	2	1,95	ns
Prog*rank	3	1,31	ns
prog*niv K*rank	6	0,15	ns

Table 4. ANOVA on K content in leaflets along different leaf rank (3,9,17,25,33). Niv K : K0,K2,K3; Prog : for progenies A and B. ALCP10 trial.

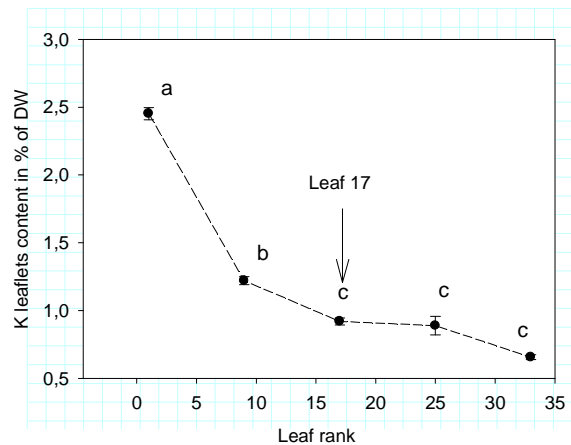


Fig. 4. Variation of K content in leaflets in % of DW along leaf ranks. a,b,c : means comparison with difference at  $P < 5\%$ . ALCP10, A progeny. BLRS analyses with corrections :  $Y = 0.11 + 0.61x$ ,  $r^2 = 0.32^{**}$ .

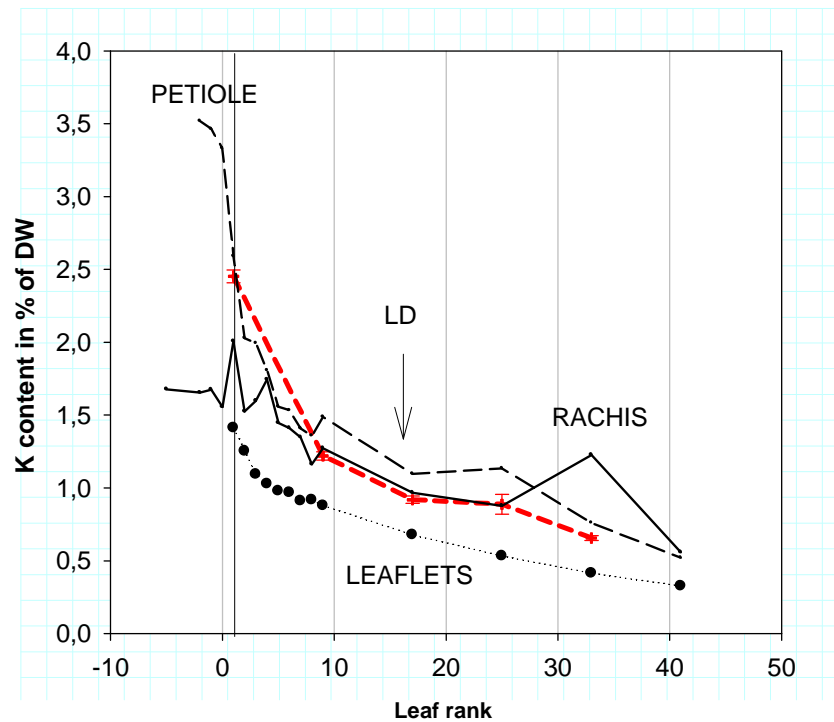


Fig. 5. Evolution of K content in K% of DW in leaflets, rachis and petioles in relation with leaf rank from rank -6 to 41. LM2T x D10D, La Mé experiment. LD for leaf diagnosis. Line separating heterotrophic phase (-10 to rank 1) to the autotrophic one. Red line is presenting the results for ALCP10 on A progeny.

Similar observation is done on the crown dissection on tree belonging to LM2T x D10D type (Fig.5). During the heterotrophic phase (rank -6 to rank 1), high K content is noticed for the rachis (2.5 %) and petioles (3.5 %) compared to those of leaf rank 1 until 41. Leaflets exhibit lower K content whatever the rank, strengthened the idea that K is mainly located in heterotrophic tissues.



## Relation of K and sugars in tissues

### K and starch

#### 1. Variation of starch along rachis length (for leaflets and rachis)

Along rachis sections (Fig.1), starch content in leaflets and rachis shows opposite tendencies in relation with K applications (Table 5, Fig.6). For leaflets, under K0, an important starch accumulation is noticed at C point (sections 1-2) near the petiole part. K content in this part is low.

starch leaflets	DF	F	Pr>F
prog	1	2,03	ns
nivK	3	3,4	+
sections	3	0,25	ns
prog*nivK	2	0,53	ns
prog*sections	3	0,04	ns
Niv K*sections	9	2,51	+
prog*nivK*sections	6	0,24	ns

Table 5. ANOVA on starch content t in leaflets along different rachis sections (1-2,3-4-5,6-7,8-9-10). Niv K : K0,K2,K3; Prog : for progenies A and B. ALCP10 trial.

In leaflets, starch content, which is higher than in rachis, seems to be quite stable whatever K application whereas, difference are observed, in rachis, between K2 in one part and K0,K3 in other part (Fig. 6). Under K2, accumulation of starch in rachis is pointed all along rachis except for the C point.

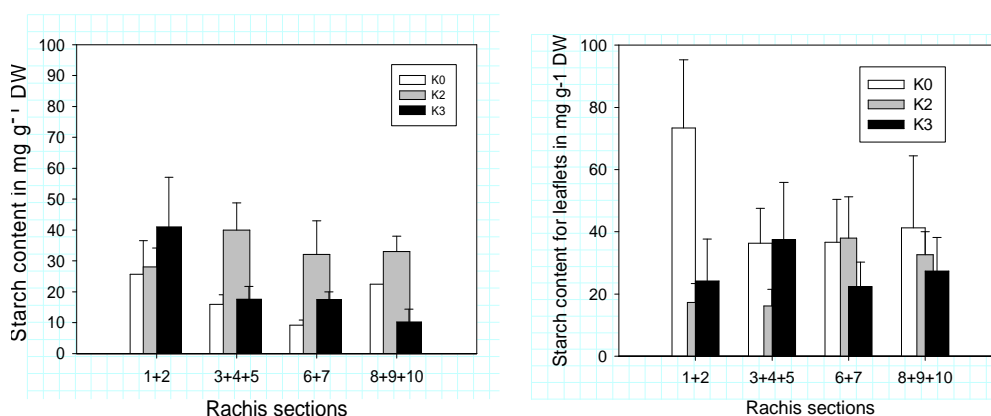


Fig. 6. Variation of starch content in mg g<sup>-1</sup> of DW along the rachis (from C to A point) for rachis (left) and leaflets (right). K0,K2,K3 : K level application in ALCP10. Results on A and B progenies are mixed.

#### 2. Variation of starch in the trunk and bunch stalk

Starch content along trunk height shows significant variations in relation with the trunk part (Table 6).

Starch trunk	DF	F	Pr>F
prog	1	0,02	ns
nivK	2	0,47	ns
location	4	11,9	***
prog*nivK	2	3,21	+
prog*loc	4	1,33	ns
nivK*loc	8	1,02	ns
prog*nivK*loc	6	0,86	ns

Table 6. ANOVA on starch content in trunk tissues depending on height (location : BASE, MIDDLE, TOP). Niv K : K0,K2,K3; Prog : for progenies A and B. ALCP10 trial.

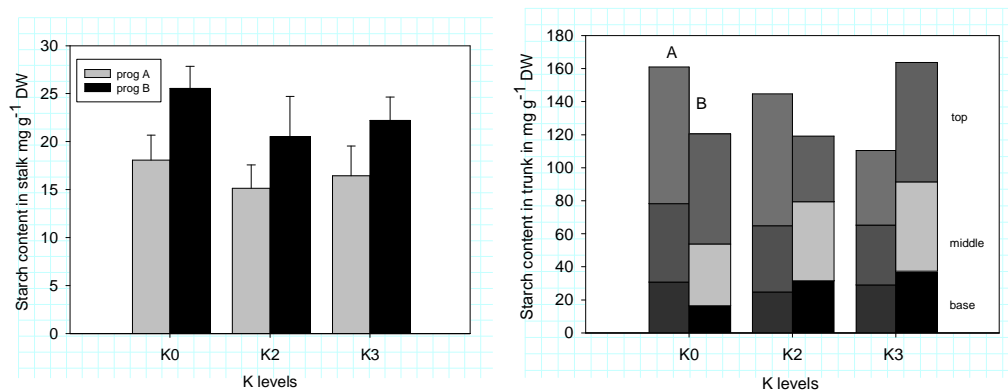


Fig. 7. Right : starch content in mg g<sup>-1</sup> of DW variation under K0,K2 and K3 application in 3 different trunk part :TOP, MIDDLE and BASE. Left : starch content in stalk for A and B progenies under K0,K2 and K3 application in ALCP10.

Starch is founded to be in higher quantity at the top of the trunk near the meristem zone (Fig. 7). A negative gradient is observed for the starch content from the top to the base of the trunk. K treatments have no significant effect on starch trunk accumulation but a tendency is still observed for the B progeny under K3 application for the base. Starch in stalk highlights significant difference between A and B progenies. B which is “K-“ shows higher starch content than A (K+) (Fig.7). Similar tendency is observed for the starch content in leaflets.

### 3. Relation between K and starch in the system « rachis-leaflets »

When the relation between the K content ratio of leaflets and rachis and the starch content ratio of the same organs is considered, a remarkable linear relation (linear regression ,  $r^2=0.95$ ,  $y = 5.06 x - 1.28$ ,  $P<0.0003$ ) can be estimated (Fig. 8). High inter-relation between K flux and sugars flux is suspected between rachis and leaflets. The arrow is indicating the sense of increase of leaflets/rachis contrast with K and starch.

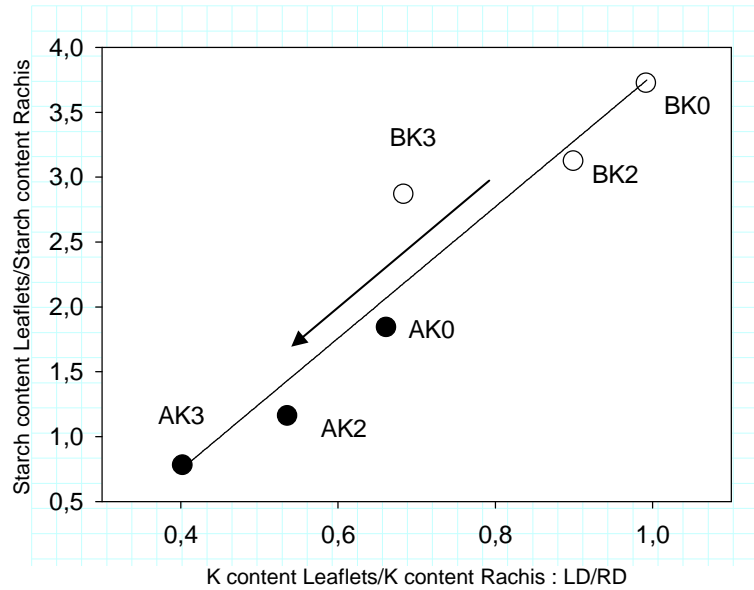


Fig.8. Linear regression between K content ratio (Leaflets/rachis) and K starch ratio (Leaflets/rachis), for A and B progenies under K0,K2,K3. Means per progenies per K levels are presented.

### *K and soluble sugars*

#### 1. Variation of soluble sugars among organs

Both K treatment levels and “organs” have strong significant effect on glucose content in tissues (Table7). Maximal glucose content is observed in the trunk base ( $66.12 \pm 12 \text{ mg g}^{-1} \text{ DW}$ ) and the petioles ( $74.23 \pm 11,1 \text{ mg g}^{-1} \text{ DW}$ ) under K0 treatment.

ANOVA	DF	Fvalue (sucrose)	P<F	Fvalue(glucose)	Pr>F
prog	1	3,03	ns	3,45	+
niv K	2	31,55	<0,0001***	39,2	<0,0001***
organe	9	41,98	<0,0001***	33,8	<0,0001***
prog*niv K	2	1,6	ns	3,36	+
prog*organe	8	0,95	ns	1,99	+
niv K *organe	16	0,25	ns	6,25	***
prog*nivK*org.	10	0,87	ns	2,57	**

Table 7. ANOVA on sucrose and glucose content for different oil palm tissues. Organs : leaflets, rachis, petioles, trunk top, trunk middle, meristem, trunk base, stalk, spikelets, roots. Niv K : K0,K2,K3; Prog : for progenies A and B. ALCP10 trial.

Strong depressive effect of K3 application is observed on glucose content in all organs, indicating a K influence on glucose circulation at tree scale (under K3, trunk base :  $39.95 \pm 7.93 \text{ mg g}^{-1} \text{ DW}$ ; petioles :  $24.72 \pm 4.2 \text{ mg g}^{-1} \text{ DW}$ ).

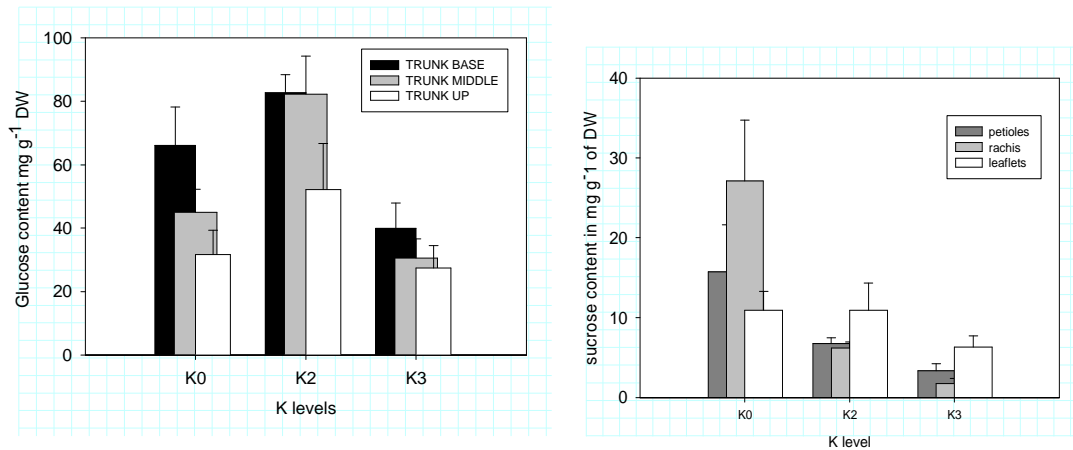


Fig.9. Left : Evolution of glucose content under K application (K0,K2,K3) for the 3 trunk compartments (BASE, MIDDLE,UP). Right : evolution of sucrose content under K application for petioles, rachis and leaflets of leaf rank 17. ALCP10.

If the evolution of the glucose stock in trunks is imperfectly clear, nevertheless some general pattern can be described : trunk base shows, whatever K treatment, maximal glucose content (Fig.9) compared to the middle and the top. Other point : under K3 application, the glucose stock is strongly reduced indicating an important use of this reserve sugar when K is added in big quantity.

Addition of K (K3) has also a strong effect on sucrose content in petiole and rachis, but not on the source (leaflets), indicating a possible increase of the sucrose circulation to the meristem.

## 2. Occurrence of K with glucose stock

If we analyse now, the repartition of K in all tissues studied and that one of glucose, interesting relation can be pointed out (Fig. 10). Maximum K content and glucose content are found in the trunk base when minimum is observed in the leaflets. It seems that K is mostly accumulated with reserve sugars (glucose) which can circulate in opposition with sucrose (maximal sucrose content in meristem, 76 mg g<sup>-1</sup> DW with quite low K) and starch (maximal starch content at the top of trunk). When observing the carbohydrates composition of all organs (Fig.11) and especially in leaflets, it is obviously starch that presents a higher concentration compared to those of glucose except in the rachis and petiole. Then looking for K in leaflets is difficult compared to rachis.

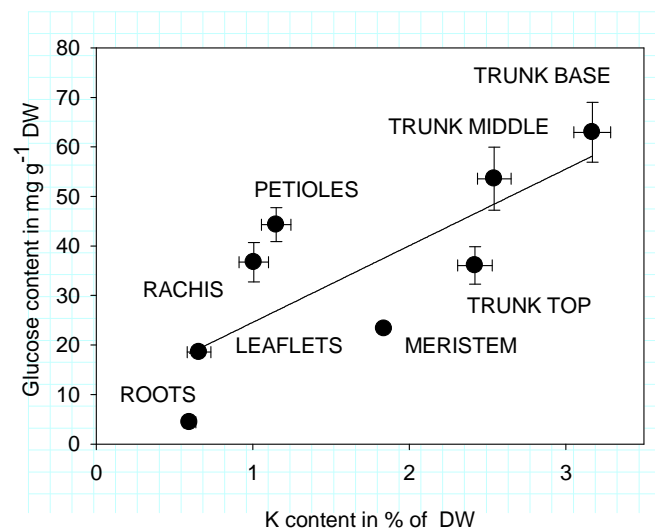


Fig. 10. Relation between K content (% of DW) and glucose content (mg g<sup>-1</sup> DW) in different oil palm tissues. Linear regression  $Y=9.09 + 15.4 x$ ,  $r^2=0.60^{**}$ .ALCP10 results.

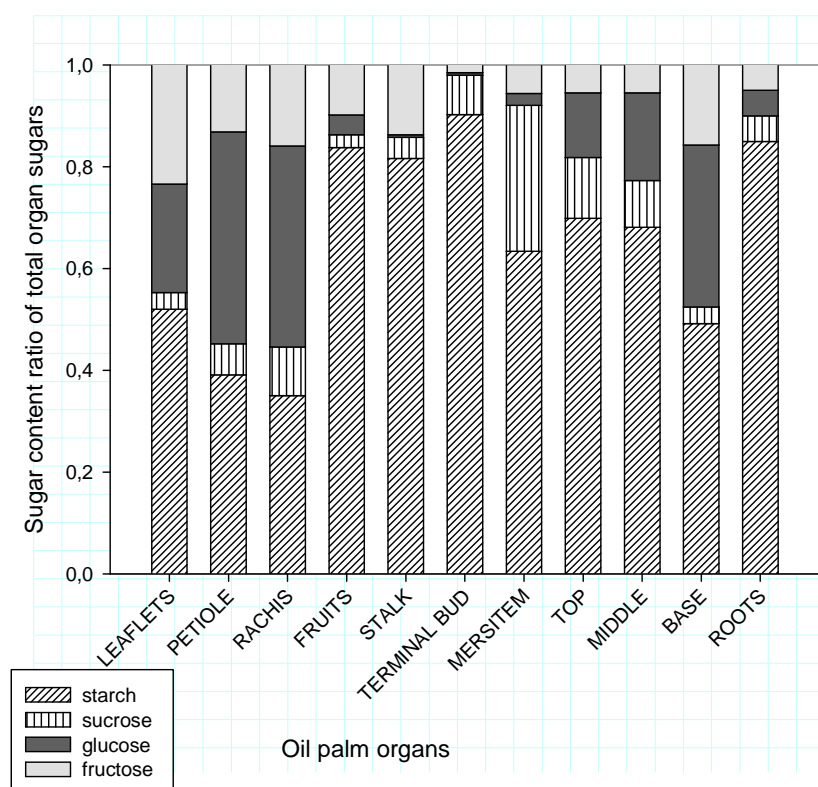


Fig. 11. Variation of the composition of the carbohydrates (starch, sucrose, glucose, fructose in % of total carbohydrates) content in all organs : ISOPALM1 data.

An amazing exception is found for the stalk of the bunch where a very important K concentration is found with high starch content.

## Discussion and conclusion

In this work, we did analyzed the K allocation in different oil palm tissues, related to carbohydrates, in order to explain why in some agronomic trials, important K accumulation is observed in rachis instead of leaflets in reference to LD (Foster, 2003).

Main results of our study concerned firstly the notification of K location preferentially in heterotrophic organs (trunk, petiole, rachis) and tissues (white parenchyma tissues in the center of the rachis and petiole) compared to photosynthetic one (leaflets). Such a result was already found by Dubos et al. (2010). Then, logically, K is also preferentially located in growing organs as young leaves which are in heterotrophic phase until almost rank 2 (Lamade et al. 2009). In our case, accumulation of K was well observed under K3 application in petioles and rachis tissues, but not in trunk. Nevertheless, in other agronomic trials (Dubos, personal communication) accumulation of K in trunk tissues can be observed after several years of K treatment. This first result may impact LD because K is not so susceptible to be accumulated in leaflets tissues compared to rachis. Then K leaflet content can still stay quite low despite high quantities of K applied. In all observations, K content, observed in rachis tissues, was better correlated to fertilizer treatment instead of leaflet tissues used in LD. K rachis was in any case a better indicator of mineral K applied for the reason enounced above. Also, taking into account all K analyses performed on all ranks, "Leaf rank 17" for K content can be considered as a good "middle estimator" of K status in crown.

The second important observation is dealing with the apparent occurrence of K in reserve tissues (as trunk base, petiole) in concomitance with a soluble sugar, the glucose, highly suspected to be the circulating sugar when starch seems to be the main carbohydrate reserve form for oil palm (Legros et al. 2009, Lamade et al., 2009). Until now, glucose dynamic for oil palm is not well understood.

Looking at glucose variation content in oil palm tissues under several K application levels has given us the opportunity to clarify its role in fruit filling. The last point is strengthened by the fact that an important K application (K3 : 4.5 kg of KCl/tree/year) affect strongly glucose stock (diminution) in trunk base and in petiole, most probably in favour of sugar flux fuelling bunch filling. As a direct consequence, a general tendency (average upon 6 years) of K application on the increase of FFB is well observed (Fig. 12) on A progeny and B progeny -that one presenting a lower response- under K3 in ALCP10 trial (Ollivier, 2014).

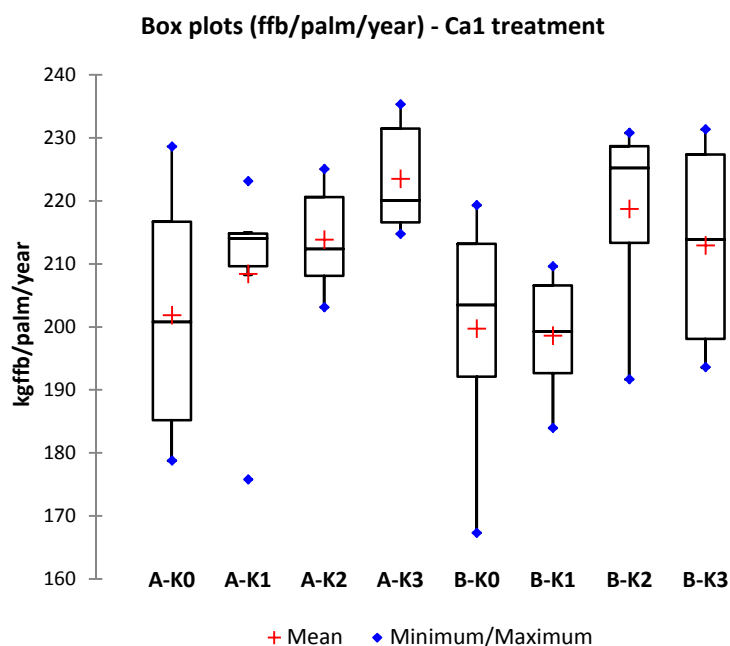


Fig. 12. Average production (upon 6 years) in kg FFB/palm/year for A and B progenies in ALCP10 trial, under K0,K1,K2 and K3 treatment. Graph : " box plot" of *proc insight*, SAS software.

Another observation (Lamade, 2014) is related to important sucrose flux from rachis and petiole to meristem zone under K3 treatments in ALCP10 trial. High K application is supposed to provoke a quick sucrose circulation from leaflets most probably directly to the meristem because no sucrose stock is observed in rachis and petiole. But still, the observation of leaflets sucrose content in ALCP10 seems quite high : if K is circulating with sucrose and H<sup>+</sup> from leaflets to the meristem zone, any sucrose accumulation in leaflets under abiotic (water deficit, mineral deficiency) and biotic stress (*ganoderma*, other as shade by overlapping of oil palm leaves) will disturb K flux, which is supposed to move very quickly thorough the cytoplasm cells. Good example of sucrose accumulation in cotton leaves have been bring Gérardeaux et al. (2010) under strong K deficiency. But in our case, any K addition by fertilization is susceptible to conduct to a low mineral response by the leaflets and possibly an accumulation of non-used K in rachis and petiole or trunk base.

This last point hence the fact that a low K response by the leaflets may be related to a metabolic reason instead of a mineral deficiency in soil or due to poor fertilization management. It is the reason why complementary metabolic analyses, when a low LD response for K is observed, could be a key to identify the problem source. If, in some cases rachis tissues is chosen as a better K indicator response for K application, still direct relation with FFB have to be better proven. K status determination via rachis K content still can stay questionable in regards of the great variability of rachis K content, highly depending on K versus soluble sugars circulations (sucrose and glucose) related to the internal oil palm metabolic dynamic. Another remark in addition to the metabolic significance of a low K content in leaflets is the unusual high sucrose content in trunk in ALCP10 oil palm trees.

The "super" strong relation between respective K leaflets/rachis ratio and starch leaflets/rachis ratio can be explained by a strong " progeny effect". Evidences were observed (Lobato et al., 2012) of a

relation between the K+/K- progenies status and their respective leaflets starch content. K+ progenies seems to be “starch-“ when K- progenies show high starch content. Here, we found similar results with A (K+) which is starch- and B (K-) which is starch+. Then, this strong “structural” relation is an argument in favor of the high link of K and reserve sugars for oil palm. Complementary experiment at bigger scale (agronomic and genetic trials) has to be undertaken to explore the new incoming directions of this present work in order to improve the Leaf and Rachis Diagnosis accuracy for K in relation with the genetic background of the new breeding material towards adequate mineral responses.

*Acknowledgements:* this work is using 3 sources of experimental data. We are firstly great full to CIRAD-UPR34 for the data set originating from La Mé Research Station (Ivory Coast). An important part of the present study is coming from the trial ALCP10 studied in the ISOPALM2 project : we thank Palmelit for funding the study and SOCFINDO Aek Loba Estate (North Sumatra, Indonesia) for their kind help in data collecting. A third part of the data is coming from the ISOPALM1 project : we thank IOPRI for all support during experimental field work at Aek Pancur Research Station (North Sumatra, Indonesia).

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